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Seed Zones and Breeding Zones for Sugar Pine in Southwestern Oregon

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Abstract

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Provisional seed zones and breeding zones were developed for sugar pine (*Pinus lambertiana* Dougl.) in southwestern Oregon. Zones are based on a map of genetic variation patterns obtained by evaluating genotypes of trees from 142 locations in the region. Genotypes controlling growth vigor and growth rhythm were assessed in a common garden. Within southwestern Oregon, two zones are recommended for low elevations (< 740 m), two zones for middle elevations (> 740 and < 1172 m), and four zones for high elevations (> 1172 m).

Keywords: Seed zones, geographic variation, genetic variation, adaptation (plant), sugar pine, *Pinus lambertiana*.

Summary

The zones presently used to guide seed transfer and breeding of sugar pine in southwestern Oregon are derived from a map prepared by the Western Forest Tree Seed Council in 1966. The council members attempted to classify the region into zones of homogeneous environment based on information from local foresters about climate, growth potential, and growth habit of indigenous tree species, primarily Douglas-fir. Seed zones ideally should be based on knowledge of the long-term effects of seed transfer; information about the genetic structure and habitat of the species is a less satisfactory base. Neither kind of information was available for sugar pine when the seed zone map was made in the early 1960's.

Satisfactory data about effects of seed transfer can come only from field tests carried to rotation age, but such tests are generally not affordable. An alternative to the long-term field test is to map genetic variation patterns as they exist in the native stands. Such a map can be used to devise provisional zones.

This paper reports new seed-transfer zones based on genetic variation patterns for sugar pine in southwestern Oregon. Seedling progeny from 200 trees from 142 locations in southwestern Oregon were grown as families in a common-garden nursery to evaluate the genotypes of the parents. Genetic variation among the families indicated that two principal components of genetic expression in several traits could be used to describe adaptive differences among populations. For each component, the variability among local populations accounted for about 50 percent of genetic variability among all families. The remaining 50 percent of genetic variation was contributed by families within local populations. Natural selection apparently has created local populations in the region that vary genetically in complex patterns along complex environmental gradients.

The zones developed from the genetic variation patterns differed greatly from the zones recommended in the Forest Tree Seed Council map. If a zone is considered as having boundaries of latitude, east-west departure, and elevation, the new zones are larger in all three dimensions. In southwestern Oregon, two of the new zones were recommended at low elevations (< 740 m), two at middle elevations (> 740 and < 1172 m), and four at high elevations (> 1172 m).

Risks of poor adaptation, which were estimated by simulated transfers within a zone, suggested that in the average seed transfer within zones, fewer than 25 percent of seedlings were likely to be poorly adapted. The estimates of risk applied only to transfers among sugar pine sites within the zone. Zones for Douglas-fir or for other species may be greatly different in size and configuration.

Contents

Introduction

The seed transfer and breeding zones that foresters and tree breeders use to restrict transfer of sugar pine (*Pinus lambertiana* Dougl.) in southwestern Oregon are derived from a seed zone map prepared by the Western Forest Tree Seed Council (Oregon [Tree Seed Zone] 1966). Although seed zones should reflect the habitat and genetic structure of the species, such information was not available in 1966 when the map was prepared. The scientific basis of zone maps for sugar pine therefore required evaluation.

Field tests are needed that evaluate performance to rotation age to define zones precisely. In the absence of other knowledge, a design that samples many seed sources and many plantation sites within the region is necessary. With anything less, results cannot be extrapolated from the test sites to the commercial sites, and zone boundaries cannot be objectively drawn. Experiments of this scale are generally unaffordable.

An alternative to extensive, long-term field testing is to map patterns of genetic variation in the native stand from short-term tests at a single site (Campbell 1986, Langlet 1945, Rehfeldt 1983, Squillace 1966). Two main assumptions are implicit if genetic maps are used to devise provisional zones: (1) genetic variation among populations reflects natural selection by an environment that varies across locations; and (2) the greater the genetic difference among populations, the greater the risk in transfers of seedlings between origins of populations. Other assumptions of this model for devising seed-transfer guidelines are discussed elsewhere (Campbell 1986). Maps can also provide a framework for sampling seed sources and plantation sites so that few long-term tests are needed to validate zone boundaries.

This paper reports the mapping of genetic variation of sugar pine in southwestern Oregon and the provisional seed zones and breeding zones derived from the map.

Materials and Methods

Cones were collected from 2 trees at 58 locations and 1 tree at an additional 84 locations for a total of 200 trees at 142 locations. The area of sampling extended north from the California-Oregon border to the latitudes of Sutherlin, Oregon (T. 25 S.), in the Cascade Range (160 km) and Cape Blanco (T. 32 S.) in the Siskiyou Mountains (90 km). The region ranged west to east from near the Pacific Ocean to the crest of the Cascade Range (R. 4 E., 170 km).

Besides the areal dimensions, seven other variables were measured to index the habitat of each tree.

1. Elevation, ranging from 300 to 1600 m but, for frequency of occurrence within elevational classes, uniformly distributed between 600 and 1400 m.

2. Aspect, uniformly distributed from 0° to 360°.

3. Slope, uniformly distributed from 0 to 65 percent.

4. Drainage direction, which might index fog propensity within the region, uniformly distributed from 0° to 360°.

5. Mean annual precipitation (Froehlich and others 1982), ranging from 73.7 to 355.6 cm and distributed with two peaks, one with a mean of 124.5 cm and the other with a mean of 289.6 cm.

6. Horizon sum, an index of general exposure, calculated as the sum of the vertical angles from the parent tree to the horizon taken at 22.5° intervals of azimuth from 0° to 360°. The sums ranged from 0 to 472 but were concentrated between 120 and 285.

7. Sun exposure on April 3, taken as the vertical angles at intervals of 22.5° east (90°) to west (270°) and plotted to provide a graph of the horizon across the southern sky. The minutes of direct sun exposure at the tree location were calculated by using this graph and the graphed path of the sun angle throughout the day of April 3; values ranged from 400 to 764 minutes with a median of 690 minutes.

We estimated genotypic values of parent trees by growing their families from open-pollinated seeds in seed germinators and in a common garden. For each of the 200 trees, seeds were separated into two 50-seed lots. We started stratification (130 days at 1.7 °C) and germination for one lot a week before the other lot to provide two replications. Lots were germinated in petri dishes at 22 °C and 14-hour days. Germinated seeds were counted daily to obtain the mean and standard deviation of germination rate (Campbell and Sorensen 1979). Germinated seeds removed during daily counts were stored at 1 °C for outplanting later in the common-garden test.

Germinated seeds from each of the 200 families were planted in four replications of four-seedling row plots in each of four nursery beds. The original plan was to impose different growth treatments on the four nursery beds. This was precluded soon after planting by an unidentified damping-off disease that caused mortality averaging 40 percent in two beds and 60 percent in the other two. We therefore attempted only two test environments: a control with no treatment for the two beds with greatest mortality and a warm soil and warm air treatment for the two beds with least mortality. We created warm soil by burying heating cables 15 cm below the soil surface. Warm air was obtained by covering beds with a polyethylene tent; this was done only in spring and autumn to extend the growing season. Temperature was not measured, but our experience with similar treatments suggests that the temperature in growth zones probably exceeded the ambient by 0 to 10 °C, depending on cloud cover and time of year.

Ideally, traits measured in the common garden should be suitable for evaluating differences in vigor and timing of growth among families. In sugar pine, determining stop and start of the vegetative cycle by "bud-burst" and "bud-set" is difficult. We anticipated, however, that differences in growth rhythm would show in the structure of genetic correlations among different segments of height extension, each segment considered as a separate trait. In the second growing season, seedling height was therefore measured 10 times, 3 to 7 days apart, (table 1), from the beginning of the extension period in April to the end in late May. In the third growing season, height was measured three times from May 25, shortly after the start of extension, to June 17, after extension had ceased. Diameter was measured once at the end of the third growing season.

The mortality in the first growing season caused drastic changes to parts of the intended analyses, and some pooling of data was necessary. We eliminated the designed replication within beds by treating seedlings within families as if they were randomly allocated rather than as being planted in row plots. Two replications were created by considering the two beds in each treatment as two blocks.

Table 1—Trait code, dates, and units of measurement of seedling traits; total height (HT), total diameter (DIA), mean germination rate of 50 seeds (DR MN), and standard deviation of germination rate (DR SD)

Code	Date measured	Measurement units
HT 21[1]	April 4-6	cm
HT 22	April 9-10	cm
HT 23	April 12-13	cm
HT 24	April 19-21	cm
HT 25	April 23-26	cm
HT 26	April 28-30	cm
HT 27	May 3-7	cm
HT 28	May 10-12	cm
HT 29	May 17-19	cm
HT 21	May 24-26	cm
HT 31	May 25-27	cm
HT 32	June 7-9	cm
HT 33	June 15-17	cm
DIA 31	December 15-22	mm
DR MN	April 13-30	(days to germination)$^{-1}$
DR SD	April 13-30	(days to germination)$^{-1}$

[1] The 1st numeral in the code designates the growing season, the 2d the place in sequence of measurements; for example, HT32 is the 2d measurement of total height in the 3d growing season.

Analyses of data from the two beds in the control treatment indicated that for most traits the within-plot variation was so large and the genetic variation so small that analyses did not help in evaluating genotypes. Analysis of the control treatment was discontinued.

The analyses of data from the warm treatment proceeded in nine steps. Seven are described in detail elsewhere (Campbell 1986) and are listed here only as a summary.

1. Analyze variance and covariance (table 2).

2. Calculate genetic correlation coefficients at the source and family within source (hereafter family) levels.

3. Reduce the dimensions in the data by a principal component analysis of the matrix of coefficients from the source level of genetic correlation.

4. For each of the significant principal components, calculate factor scores for each source and family.

Table 2—The partition of variation among seedlings into sources of variation, and the expected mean squares used in estimating components of variance

Source of variation	Degrees of freedom	Expected mean squares [1]
Total	3,647	
Replications	1	
Sources	141	$\sigma_w^2 + 18.20\,\sigma_{f(s)}^2 + 25.66\,\sigma_s^2$
Families in sources	58	$\sigma_w^2 + 18.20\,\sigma_{f(s)}^2$
Within plots	3,447	σ_w^2

[1] σ_s^2 = variance of seed-source effects;

$\sigma_{f(s)}^2$ = variance of effects of families within seed source; and

σ_w^2 = variance of within-plot effects.

5. Describe the pattern of genetic variation in factor scores for each principal component by a regression analysis (backward stepwise, Draper and Smith 1966) that uses indices of the parent-tree habitat as predicting variables. The preliminary model included quadratic and interaction terms suggested by previous experience (Campbell 1979, 1986) for some variables in addition to linear terms for all variables.

6. Calculate lack of fit using variation among families at a location as pure error (Draper and Smith 1966).

7. Calculate an index of risk in seed transfer—risk is the fraction of non-overlap between factor-score distributions for native and introduced seed sources.

We added two other steps, a cluster analysis and a new procedure for assigning boundaries to seed zones. The first was tried because of significant lack of fit to the regression model. We thought the second was needed because a change from previous procedures (Campbell 1986) would make the resulting seed zones more easily used by foresters.

Lack of fit could not be rectified by common procedures. Therefore, in addition to scattergrams of residuals with location variables (Draper and Smith 1966), deviations from the models were clustered using McIntire's (1973) algorithm and computer program (MACLUS, Computer Center, Oregon State University). Though unlikely, deviations might vary jointly in patterns not otherwise obvious in the residuals.

The second new step was a procedure to provide zones with boundaries determined only by the customary geographic and elevational limitations. The resulting zones were somewhat larger than zones developed in strict compliance with genetic variation patterns, but they should be easier to use in practice. The procedure had five parts.

1. On a map, pinpoint locations at low, middle, and high elevations in each township (9.65 by 9.65 km) within the region.

2. Record all pertinent habitat variables at each of 629 locations.

3. Use the regression equations for describing genetic variation patterns to calculate factor scores at each location.

4. Divide the region into tentative zones based on visual inspection of genetic variation patterns.

5. Calculate risk values (Campbell 1986) for 200 hypothetical transfers between randomly chosen pairs of locations within each tentative zone.

Steps 4 and 5 were repeated until zones were defined in which fewer than 5 percent of the simulated transfers created risks greater than 0.5. The average risk associated with seed transfers within zones was less than 0.25. Within such zones, about 25 percent of the seedlings planted are expected to be poorly adapted in comparison to the indigenous seedlings.

Results

We partitioned variation among seedlings into effects of seed sources (σ^2_s), families in sources ($\sigma^2_{f(s)}$), and variation within plots (σ^2_w), which included variation within rows and among rows in beds. With one exception (standard deviation of germination rate of seeds), all traits differed among sources and families. In the second growing season, an average of 6.0 percent of the variance in height traits could be attributed to source, 7.9 percent to families, and 86.1 percent to within-plot (table 3). In the third growing season, more of the average variance in height and diameter was found among sources (10.2 percent) and less among families (6.1 percent) and within plots (83.7 percent). Throughout the third growing season, variation among sources increased steadily and variation among families and within plots decreased steadily (table 3). This apparent trend was based on only three measurement periods, which sampled early, middle, and late phases of extension growth.

The largest part of the variation among seedlings occurred within plots; some was the result of genetic variation among individuals within a family. For this paper, the genetic variation within plots was assumed to be two-thirds of the additive genetic variance. Sugar pine usually grows in isolated, small stands where pollination probably includes selfing or crossing between near relatives. The genetic correlation among family members is therefore probably nearer to 0.33 than to 0.25. Given a correlation of 0.33, the additive genetic variance (σ^2_A) is $3\ \sigma^2_{f(s)}$ 2 and the amount within plots is $2\ \sigma^2_{f(s)}$; that is:

$$\sigma^2_A - \sigma^2_{f(s)} = 2\ \sigma^2_{f(s)}\ .$$

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Table 3—Analysis of variance of traits and of factor scores of principal components (PC-1 and PC-2)

Trait[1]	Mean	Total variance[2]	Percentage of total variance			
			Among sources	Among families	Within families	Among plots
HT 21	7.22	3.197	6.9**	8.2**	84.9	
HT 22	9.20	4.169	7.4**	7.4**	85.2	
HT 23	9.69	4.710	5.7*	8.4**	85.9	
HT 24	10.25	5.318	6.1**	7.2**	86.6	
HT 25	10.90	6.331	5.2*	7.6**	87.2	
HT 26	11.79	7.496	5.2*	7.8**	87.1	
HT 27	12.35	8.668	5.3*	8.1**	86.7	
HT 28	12.89	9.317	5.4*	7.7**	87.0	
HT 29	13.48	10.567	6.5**	8.2**	85.3	
HT 210	13.45	10.597	6.3*	8.3**	85.4	
HT 31	18.14	21.964	8.8**	8.6**	82.6	
HT 32	37.62	77.958	11.6**	6.1**	82.4	
HT 33	39.92	77.390	12.8**	5.4**	81.9	
DIA 31	10.06	4.290	7.7**	4.4**	87.9	
DR MN	.38	.055	48.4**	8.9*		42.8
DR SD	.24	.020	38.3*	8.0		53.7
PC-1	15.70	12.833	10.2**	8.6**	81.2[3]	
PC-2	2.50	3.153	27.8**	28.3**	44.0[3]	

* = 0.05 < P > 0.01; ** = P < 0.01

[1] Trait code and measurement units as in table 1.

[2] Total variance for HT, DIA, PC-1 and PC-2 is among-source variance (σ^2_s) + among-family variance ($\sigma^2_{f(s)}$) + within-family variance (σ^2_w). Total variance for seed traits is $\sigma^2_s + \sigma^2_{f(s)} + \sigma^2_p$ where σ^2_p represents variance of plot effects.

[3] In calculating factor scores for individual seedlings, seed traits were taken as having no variation within plots.

For the 10 height traits in the second growing season, this additive variance represented an average of 18.2 percent of within-plot variance. The additive genetic variance within plots decreased from 21 percent to 15 percent to 13 percent of within-plot variance in the three successive height measurements of the third growing season. The remaining variation was nonadditive genetic variation and environmental variation. Variable spacing among seedlings caused by first-year mortality probably contributed to the large size of the nongenetic variation.

When genetic correlations were calculated among growth traits, those calculated at the source level of variation were about 50 percent larger than those at the family level (table 4). At the source level, some coefficients were larger than one. We could not determine whether this was caused by an underestimate of genetic variance or by an inflation of covariance because of unclassified elements of common environment.

Table 4—Genetic correlation coefficients; above diagonal for seed sources, below diagonal for families

Trait	HT 21	HT 25	HT 210	HT 31	HT 32	HT 33	DIA 3	DR MN	DR SD
HT 21		0.920	0.845	1.026	0.890	0.917	1.049	0.474	0.155
HT 25	0.769		.988	.973	.982	.963	.986	.700	.396
HT 210	.855	893		1.004	1.056	1.054	1.031	.555	.390
HT 31	.386	.653	.621		.962	.948	.908	.427	.123
HT 32	.331	.531	.623	.810		1.009	.999	.136	.034
HT 33	.311	.568	.633	.923	.965		.960	.170	.005
DIA 3	.140	.438	.574	.853	.853	.912		.125	.047
DR MN	-.583	-.664	-.715	-.413	-.356	-.410	-.263		1.167
DR SD	-.361	-.434	-.560	-.141	-.319	-.268	-.248	.595	

Correlations between seed and growth traits at the source level were uniformly positive, and those at the family level were uniformly negative (table 4). Larger heights and diameters of seedlings were associated with faster rates of germination of seeds at the source level but with slower rates at the family level. Consistently more variation was found among individual seeds within those lots with faster mean germination rates. This correlation was stronger at the source level than at the family level.

To simplify interpretation of genetic variation patterns, the intercorrelated growth and seed traits were reduced to fewer dimensions by principal component analysis. The genetic correlation matrix at the source level was used as input. The correlation matrices at source and family level were different and the adaptational problems connected with seed transfer were probably more closely connected with source variation than with family variation.

The first two principal components explained about 95 percent of the variation in all traits (table 5). The first component (eigenvalue 14.076) explained six times as much of the variation as did the second component (eigenvalue 2.195). Loadings indicated that factor scores of the first principal component (PC-1) were larger in families with a larger final stem diameter and in families that were taller at all measurement periods. Larger factor scores in the second principal component (PC-2) mainly reflected large mean germination rates of seed and larger variation in rates among seeds (table 5). But factor scores for PC-2 were also larger when seedlings were larger at some periods of the second growing season (for example, traits 23, 25, 28) and smaller if seedlings were larger at other periods (for example, traits 21, 24, 26). The second principal component therefore also may reflect a pattern of extension growth that was quasi-sinusoidal within the growing season and different among sources.

Table 5—The two main principal components (PC), their loadings with traits, the variance of their factor scores (eigenvalue), and their contribution in explaining variation among all traits (as a percentage)

Trait	PC-1[1]	PC-2[2]
HT 21	0.934	-0.109
HT 22	.970	-.023
HT 23	.990	.025
HT 24	.987	-.034
HT 25	1.002	.108
HT 26	.992	-.066
HT 27	1.019	.058
HT 28	1.018	.124
HT 29	.999	.068
HT 210	1.003	.016
HT 31	.980	-.122
HT 32	.979	-.300
HT 33	.975	-.294
DIA 3	.988	-.296
DR MN	.541	.940
DR SD	.308	.990

[1] Eigenvalue, 14.076; percentage of total variation, 82.6.

[2] Eigenvalue, 2.195; percentage of total variation, 12.9.

The factor scores (PC-1 and PC-2) varied significantly (P $<$ 0.01) among sources and families in sources (table 3). The variance among sources (σ_s^2) accounted for 54 percent of the total variance among all families ($\sigma_s^2 + \sigma_{f(s)}^2$) in PC-1. This variability among all families represented, in turn, 19 percent of the variation in PC-1 among all seedlings. Sources accounted for 49 percent of variance among all families in factor scores of PC-2. An unbiased estimate of the percentage of variation in PCs among seedlings within plots was not possible. Because seed traits were measured in germinators rather than in the cold-frame plots, seed traits had to be treated as having no variation within plots in calculating factor scores. The within-family variations in factor scores therefore does not include a contribution from within-family variation in seed traits. The estimate of within-family variance is affected very little for PC-1 but greatly for PC-2 (table 3).

Differences among sources were only partly associated with habitat variables at the source origin. Regression equations relating factor scores of families to habitat variables explained 31 and 26 percent of sums of squares for PC-1 and PC-2, respectively. A large part of the remaining "unexplained" variability resulted from the large difference in factor scores between the two trees sampled at 58 of the 142 locations. Even after taking this into account, though, there was still significant lack of fit to the equation (table 6). For the occurrence of lack of fit to have been judged nonsignificant (for example, lack of fit, P $>$ 0.10), the respective equations for PC-1 and PC-2 would have had to account for at least 39 and 36 percent of the sums of squares.

Table 6—Regression analyses of factor scores from principal components

	Principal component 1				Principal component 2		
Variable[1]	Partial coefficient	Significance P<....	Standardized coefficient	Variable[1]	Partial coefficient	Significance P<....	Standardized coefficient
D	0.3986E-01	0.000	1.16	LDE	-0.8384E-06	0.000	-0.63
E	-.5959E-02	.000	-1.00	DA	-.3223E-02	.045	-.13
D^2	-.2478E-03	.000	-.96	D	-.1106E-01	.000	-.43
DE	.7132E-04	.001	.93	LE	.7475E-04	.000	.62
EDR	-.94879E-06	.011	-.58	CONST	3.0765	.000	
ER	.4918E-04	.013	.53				
CONST	14.9006	.000					

Probability of lack of fit for PC-1 is 0.024; R^2 = 0.31.

Probability of lack of fit for PC-2 is 0.020; R^2 = 0.26.

[1] Where: E = elevation in meters (-1.000);
   L = distance south to north in kilometers (-4,700) taken from Geological Survey maps
     (Oregon [Topographic] 1976);
   D = distance west to east in kilometers (-425) from above maps;
   R = annual precipitation in inches (2.54 cm) from Froehlich and others (1982);
   A = aspect in cosine (degree azimuth); and
   CONST = constant.

Residuals from the equations were examined in attempts to eliminate lack of fit. The residuals represented deviations from the regression equation of genotypic values of 200 parent trees, including the pairs of trees from 58 locations. Each tree had two genotypic values (and residuals), the factor scores of PC-1 and PC-2.

Conventional methods for examining residuals (Draper and Smith 1966) did not reveal patterns in the deviations. We therefore used cluster analysis to determine if homogenous groups of deviations were contributed by trees that were also homogenous in some identifiable aspect of their habitats. During clustering, the pooled within-group sums of squares decreased steadily when observations were factored into smaller and smaller groups until a minimum was reached when about 20 clusters had been formed.

The 20 clusters were homogenous in characteristics of factor scores within clusters but were extremely heterogenous in the origin of trees. Only 6 of the 58 pairs of trees were found together within clusters, 1 pair in each of 6 different clusters. Individuals within clusters commonly were from widely scattered locations within the region. On other occasions, trees from two clusters that were greatly different in the size and sign of the included deviations might be of similar origin. The deviations were therefore not patterned in any predictable manner, in respect to either the apparent relation among trees or the origins of trees. The significant lack of fit indicated that groupings of deviations of PC-1 or PC-2 should be expected. Apparently these groups were not connected with one another or with any readily identifiable features of the habitat of parent trees.

Predictions from regression equations indicated that variation in PC-1 was associated with the annual precipitation, elevation, and distance from the ocean of the origin of parent trees. Factor scores for trees at lowest elevations were smaller in areas of highest precipitation nearest the ocean and in areas of lowest precipitation farthest from the ocean (fig. 1A). The trend with precipitation was reversed for trees at highest elevations; factor scores were smallest in areas of lowest precipitation nearest the ocean and in areas of highest precipitation farthest from the ocean (fig. 1D). Very little genetic variation existed among trees in a broad central band of elevations (fig. 1, B and C). Within this band, factor scores were slightly smaller in the western part of the region.
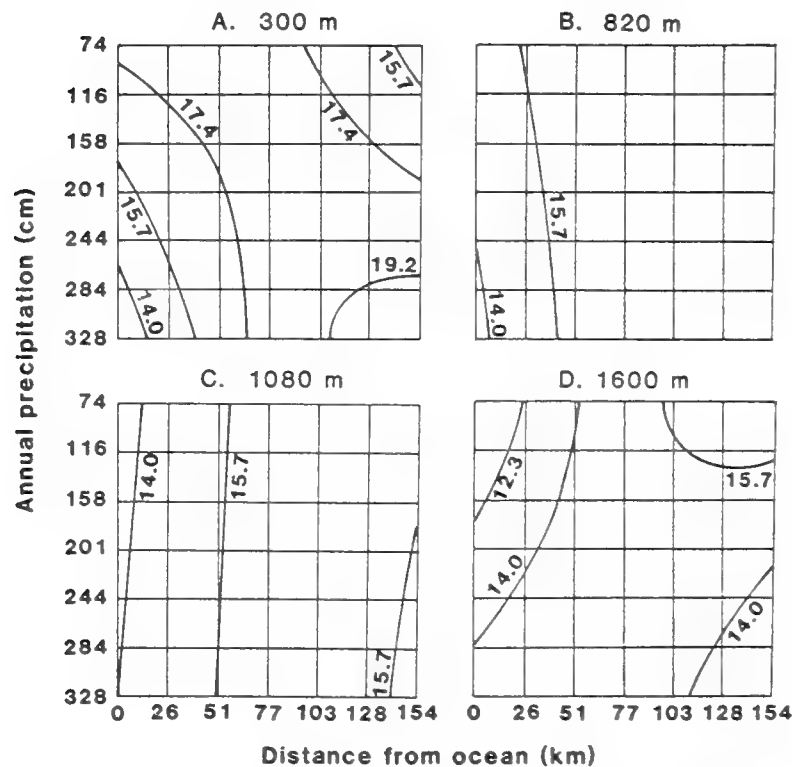
Figure 1—Factor scores (isolines are labeled with score values) of the first principal component: (A) sites at 300 m, (B) sites at 820 m, (C) sites at 1080 m, and (D) sites at 1600 m.

Trees differed in PC-2 depending on elevation, latitude, and distance of trees from the ocean. Factor scores of trees at lowest elevations were smallest in the central part of the region and largest toward the southeast and northwest (fig. 2A). Some fairly steep gradients exist from north to south in the western part of the region. For trees at the highest elevations, factor scores were smallest in the southwest and northeast and largest in the northwest. The gradient was therefore found in the western part of the region (fig. 2D). With PC-2, as with PC-1, little genetic variation was found among trees throughout the region within a broad intermediate band of elevations. Within this band, the largest scores were found in the west (fig. 2, B and C).
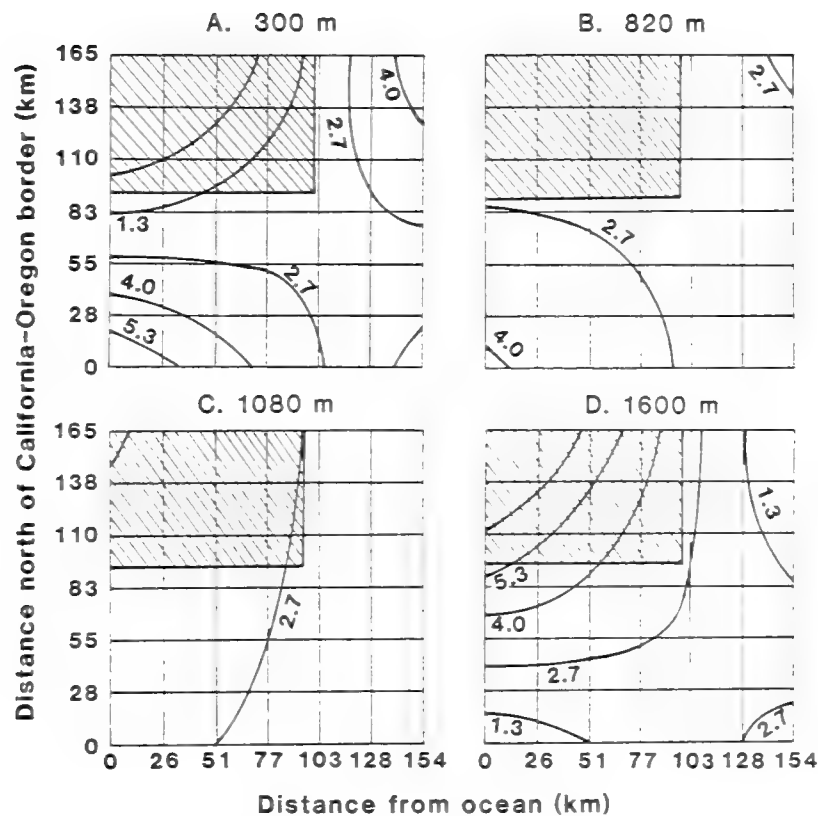
Figure 2—Factor scores (isolines are labled with score values) of
the second principal component: (A) sites at 300 m, (B) sites at
820 m, (C) sites at 1080 m, and (D) sites at 1600 m. Sites in the
hatched area were sampled minimally or not at all.

Creating eight zones divided southwestern Oregon into areas in which fewer than
5 percent of transfers involved risks greater than 0.5 (table 7). Two zones were needed
for low elevations (< 740 m), two for middle elevations (> 740 m and < 1172 m), and
four for high elevations (> 1172 m). The average transfer within a zone had a risk of
< 0.25, and only about 2 percent of transfers had risks greater than 0.5. The distribu-
tion of risks of hypothetical transfers within zones was typically bell shaped with a
slight positive skew (fig. 3). The boundary between the east and west zones at low
elevations (fig. 4) fell on the isohyetal line of 152 cm of annual precipitation, which
wanders north and south primarily within the townships in R. 8 W. (Froehlich and others
1982). For practical reasons, and because practical and biological objectives
coincided, other borders were placed along major highways within the region (fig. 5
and 6).

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Table 7—Statistics of predicted risks in 200 simulated transfers within each of the 8 provisional seed and breeding zones

Zone[1]		Transfer risk		Percentage of transfers with risks greater than indicated[2]	
		Average	Maximum	Percent	$> M_i$
Low 1	($<$ 740 m)	0.245	0.600	2	0.493
Low 2	($<$ 740 m)	.241	.628	2	.516
Middle 1	($>$ 740 m and $<$ 1172 m)	.213	.582	1	.479
Middle 2	($>$ 740 m and $<$ 1172 m)	.156	.423	0	.423
High 1	($>$ 1172 m)	.133	.450	0	.450
High 2	($>$ 1172 m)	.198	.619	2	.509
High 3	($>$ 1172 m)	.227	.569	2	.508
High 4	($>$ 1172 m)	.189	.618	1	.508

[1] See figures 4, 5, and 6 for locations of zones.

[2] By the mismatch index (M) in the ith zone; for example, if i = low 1, then 2 percent of 200 simulated transfers in low 1 had predicted risks greater than M = 0.493.
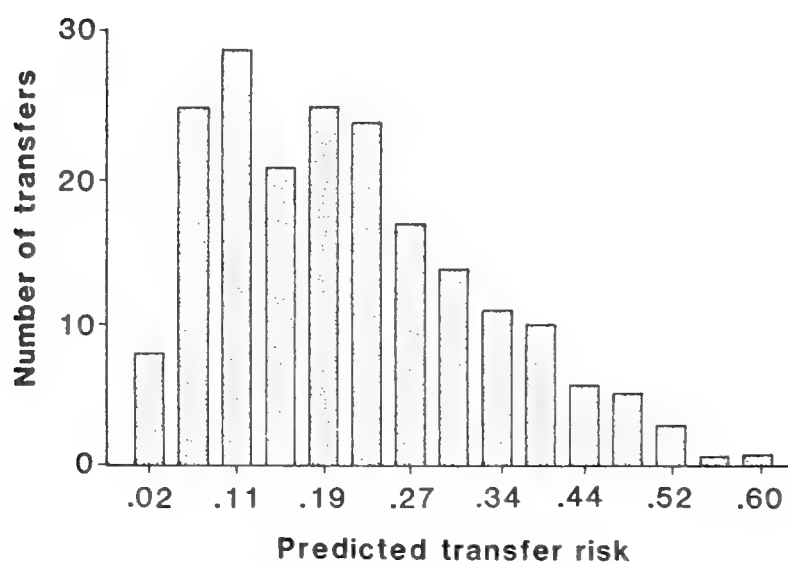
Figure 3—Distribution of variation in predicted risks for 200 hypothetical transfers within midelevation zone 1.
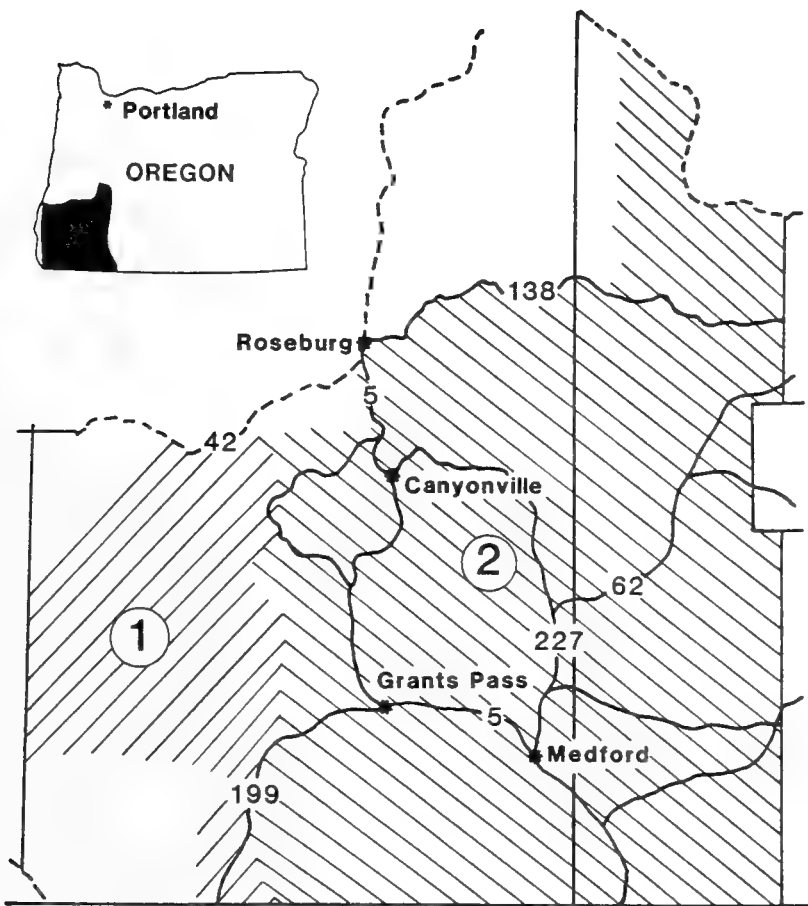
Figure 4—Provisional seed-transfer and breeding zones for sugar pine at low elevations (< 740 m). Zones 1 and 2 are designated by diagonal hatching with lines in zone 1 running perpendicular to lines in zone 2. The small numbers 5, 42, 62, etc., refer to Federal and State highways within southwestern Oregon.
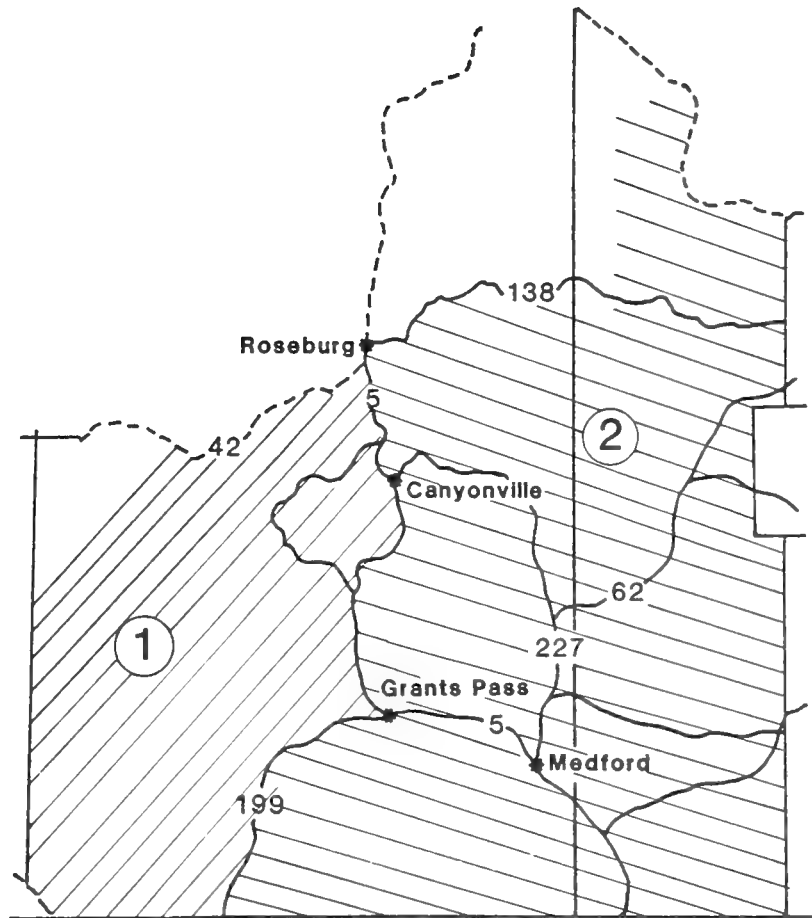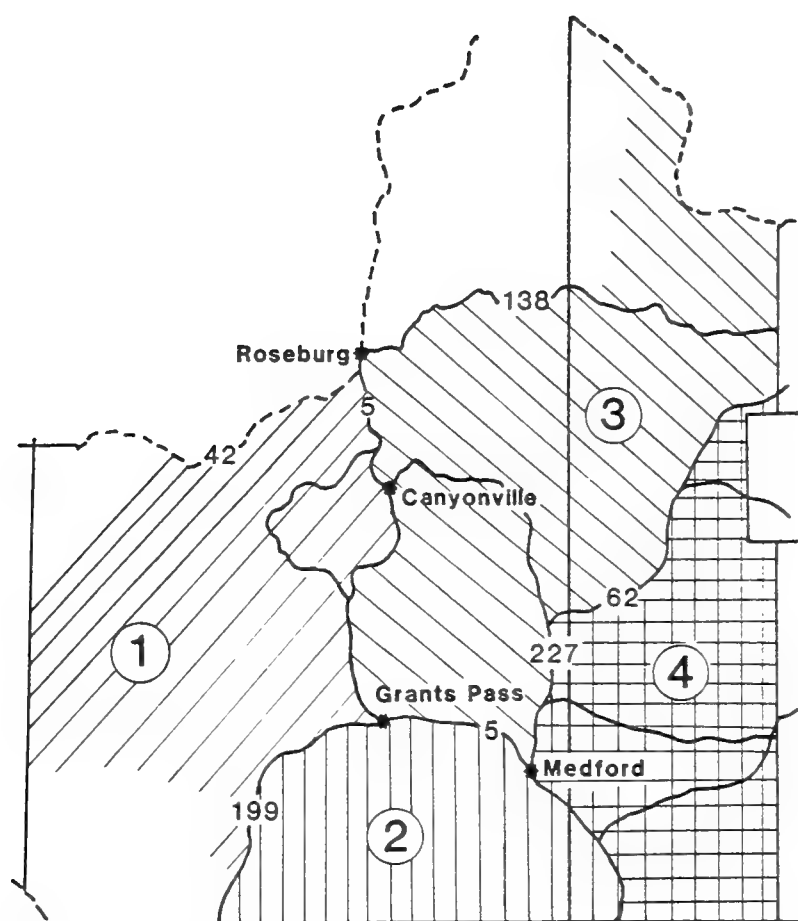
Figure 5—Provisional seed-transfer and breeding zone for sugar pines at middle elevations (> 740 m and < 1172 m). Zones 1 and 2 are designated by diagonal hatching with lines in zone 1 running perpendicular to lines in zone 2. The small numbers 5, 42, 62, etc., refer to Federal and State highways within southwestern Oregon.

Figure 6—Provisional seed-transfer and breeding zones for sugar pines at high elevations (> 1172 m). Zones 1 to 4 are designated by hatchings of different types. The small numbers 5, 42, 62, etc., refer to Federal and State highways within southwestern Oregon.

Discussion

The dimensions of the seed zones we recommend depend on a particular conceptual model of the relation of adaptation and seed transfer. Assumptions and other features of the model are discussed elsewhere (Campbell 1986). Only those aspects relevant to limits of transfer are discussed here.

The basic tenet of this model is that only a proportion of any transferred group of seedlings will be well adapted in comparison to the adaptation of seedlings within the indigenous seed supply. Furthermore, well-adapted trees are assumed to be better able to use the resources and conditions of the site than are poorly adapted trees. Poorly adapted trees will therefore be less productive over an average of years, generations, and sites than will well-adapted trees.

If well-adapted trees are more productive than less well-adapted trees, then the distribution of adapted trees within a plantation is important. The best adapted trees should be distributed throughout the plantation. If we define a spacing subunit (for example, 4 by 4 m) as the area occupied by one crop tree, then ideally every spacing subunit should include at least one well-adapted tree.

The well-adapted seedlings in a transferred seedling lot cannot be identified at planting. Planting more seedlings per hectare is the only procedure available for increasing the probability that a well-adapted seedling will be planted in a spacing subunit. The larger the proportion of poorly adapted seedlings in a lot, the larger the number of seedlings needed per crop tree. The calculations of this number provided the basis for limiting seed transfer within seed zones in our study.

The probability of a well-adapted seedling being planted within a spacing subunit is less than one—a reasonable upper limit is $P = 0.98$. Hypothetically, this upper limit will ensure greatest site productivity but at the cost of planting several seedlings per crop tree. We assumed a maximum investment of five or six planted seedlings per crop tree.

The maximum investment dictates the maximum mismatch index (M) permissible within a seed zone. The maximum index is calculated from the relationship:

$$P = 1 - Q^{N/C};$$

where:

P = the probability of an adapted seedling being included in a spacing subunit, 0.98 in this case;

$Q = 1 - S(1-T)(1-M)$;

N = the number of seedlings to be planted for a given number of crop trees per hectare (C);

C = crop trees per hectare;

S = the proportion of seedlings surviving the early establishment period;

T = the proportion of seedlings removed in early thinnings; and

M = the mismatch index—the proportion of planted seedlings that are poorly adapted relative to seedlings in the indigenous population.

Then, the number of seedlings required per hectare is:

$$N = \frac{\log (1-P)}{\log Q} \; C \;.$$

But for our purposes, the influence of early regeneration success and thinning was ignored, so $S = 1$, $T = 0$. Also, only the number of seedlings needed per crop tree (n) was of interest. Therefore:

$$n = \frac{\log (1-P)}{\log M} \;.$$

From this, if the maximum M is 0.50, the maximum number of seedlings invested per crop tree is 5.6.

One implication of the model is that any retreat from the maximum investment of seedlings per crop tree will reduce productivity. Calculations of this investment are more useful, however, as indicators of possibilities rather than as a prescription. Theoretical reasons have been given for not always expecting maximum productivity from the indigenous populations (Namkoong 1969). Other work (Braathe 1953) indicates that total harvest volume yield may not be greatly reduced by the patchiness in regeneration that could result from maladaptation, although the harvest quality may be considerably affected. Even if it is important that all crop trees are well adapted, economic reasons may demand planting fewer than 5.6 seedlings per crop tree. The average mismatch index, M, in the recommended zones was about 0.25; consequently, for the average transfer at $M = 0.25$, the planting of 2.8 seedlings per crop tree would ensure adapted crop trees. In these cases, planting more than 2.8 seedlings may be an unnecessary regeneration cost. These numbers assume complete success in regeneration and no early thinning; if either condition does not hold, the model indicates a larger number of seedlings per crop tree should be planted. Several items, other than adaptation, must be considered in any prescription for regeneration within seed zones.

How adequate the seed zones are will depend partly on how well the experiment fulfilled the assumptions the genetic mapping procedure was based on (Campbell 1986). Results from this experiment require three qualifications. First, the samples of locations were not evenly distributed throughout the region. Sugar pine tends to grow in small stands, which were more concentrated in the southwestern part of the region. More samples per unit area were taken in the southwest, so sampling tended to be proportional to the occurrence of the species rather than to area. Predictions from regression and therefore the delimitation of zone boundaries are more reliable for the western part of the region than for the eastern.

The second qualification results from problems encountered in growing seedlings in common gardens. Because of mortality, seedling genotypes were evaluated in only one environment. This limits the expression of gene effects in quantitative traits. Some genetic differences among sources may not have been manifested (Campbell and Sorensen 1978). If so, seed source variation has been incompletely characterized, and risks within zones may have been underestimated.

The third and most serious qualification is lack of fit to the regression model. A substantial amount of source variation was not accounted for by regression. Futhermore, the deviations from the model were not clustered in patterns related to geography of source origin. The source deviations could result from natural selection, but they could just as easily result from random genetic drift. If variation is caused by natural selection, risks within zones are underestimated. Making the zones smaller would not decrease the bias, however. The variation not accounted for by regression could not be ascribed to geography and therefore would not be reduced by making the zones smaller in any of the dimensions commonly used for seed-zone delimitation. Differentiation of populations by genetic drift is more likely in sugar pine then in many other species because sugar pine tends to be found in small, isolated stands. Variation caused by genetic drift should not affect zone boundaries because the differences among sources would not be predictable, adaptive differences.

The recommended zones are provisional. High seedling mortality in the common-garden test and lack of fit in the regression model have made this effort less satisfactory than it might have been. The delineation of zones did, however, incorporate all available quantitative information about genetic and habitat variation of sugar pine in southwestern Oregon. The zones, therefore, will minimize risks within the context of present information. But the information should be added to by other experiments and verified by long-term tests.

Acknowledgments

English Equivalents

When given:	Multiply by:	To find:
Meters (m)	3.282	Feet
Kilometers (km)	0.621	Miles
Hectares (ha)	2.471	Acres
Celsius (°C)	1.8 (and add 32)	Fahrenheit (°F)

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Provisional seed zones and breeding zones were developed for sugar pine (*Pinus lambertiana* Dougl.) in southwestern Oregon. Zones are based on a map of genetic variation patterns obtained by evaluating genotypes of trees from 142 locations in the region. Genotypes controlling growth vigor and growth rhythm were assessed in a common garden. Within southwestern Oregon, two zones are recommended for low elevations (< 740 m), two zones for middle elevations (> 740 and < 1172 m), and four zones for high elevations (> 1172 m).

Keywords: Seed zones, geographic variation, genetic variation, adaptation (plant), sugar pine, *Pinus lambertiana*.

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